

STUDIES ON THE TETRACLITIDAE (CIRRIPEDIA: THORACICA): REVISION OF *TETRACLITA*

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ABSTRACT. — *Tesseropora* and *Tetraclitella*, subgenera of *Tetraclita*, are elevated to full generic status in the absence of intergrading major characters. *Newmanella* gen. nov. is proposed for *Tetraclita* (*Tetraclita radiata* (Bruguiere, 1789) and *Tesseroplax* gen. nov. for *Tetraclita* (*Tesseropora*) *uniseimita* Zullo, 1968. On the basis of shell characters the five genera here recognized fall into two groups. Monometric growth, allometry of the carina, and non-tubiferous radii characterize *Tesseropora*, *Tesseroplax*, and *Tetraclita*; diametric growth, isometry of the wall plates, and tubiferous radii characterize *Tetraclitella* and *Newmanella*. Both *Tesseroplax* and *Tetraclita* are considered later derivatives from the *Tesseropora* stock; but *Tetraclitella* and *Newmanella* from a tesseroporan precursor. New distributional records for *Newmanella radiata* include the Bahamas, Puerto Rico, Dominica, and Venezuela. Apparently the antenniform ramus of cirrus III in *N. radiata* plays some role during the reproductive cycle, but its exact function is unknown.

RESUMEN. — *Tesseropora* y *Tetraclitella*, subgénero de *Tetraclita*, están elevados al estado genérico en ausencia de intergradación caracteres mayores. *Newmanella* gen. nov. está propuesto para *Tetraclita* (*Tetraclita radiata* (Bruguère, 1789) y *Tesseroplax* gen. nov. para *Tetraclita* (*Tesseropora*) *uniseimita* Zullo, 1968. En el base de caracteres de concha los cinco géneros reconocidos aquí, caen en dos grupos. Crecimiento monométrico, alometría de la carena, y radios no-tubífero caracterizan *Tesseropora*, *Tesseroplax*, y *Tetraclita*; crecimiento diamétrico, isometría de la láminas de las paredes, y radios tubífero caracterizan *Tetraclitella* y *Newmanella*. Los dos *Tesseroplax* y *Tetraclita* son considerados derivativos más tarde de los progenitores de *Tesseropora*, pero *Tetraclitella* y *Newmanella* de un progenitor de *Tesseropora*. Registros distribucionales nuevos por *Newmanella radiata* se incluyen las Bahamas, Puerto Rico, Dominica, y Venezuela. Aparentemente, la ramal antenniforma de cirrus III en *N. radiata* hace un papel durante los reproductivos, pero su función exacto es desconocido.

The Tetraclitidae comprise a group of intertidal balanomorph barnacles occurring in tropical and warm-temperature waters between latitudes 38° north and 52° south. Although these barnacles are a major component of intertidal faunas they have not received adequate attention either taxonomically or biologically. In this, the first in a series of papers covering the taxonomy and general biology of the tetraclitids, I re-evaluate the status of *Tetraclita* and its subgenera, and propose a new classification in the light of recent studies (Ross, 1968), and the work of Darwin (1854), Nilsson-Cantell (1921) and Hiro (1939).

There are more than two dozen named taxa distributed presently between *Tetraclita* Schumacher, 1817 (type species: *T. (Tetraclita) squamosa* (Bruguiere), 1789), and its subgenera, *Tesseropora* Pilsbry, 1916 (type species: *T. (Tesseropora) rosea* (Krauss), 1848), and *Tetraclitella* Hiro, 1939 (type species: *T. (Tetraclitella) purpurascens* (Wood), 1815). These subgenera are distinct, and their elevation to generic status clarifies relationships that are obscured when all of the species are considered monogenic.

Both Darwin (1854: 344) and Hiro (1939: 270) cited numerous morphological characters that support the generic distinctness of the Caribbean western Atlantic species, *T. radiata*. These characters, coupled with the absence of intergrading major morphological structures, necessitate the proposal of *Newmanella* gen. nov. for this species. Attempts to assign the recently described Pliocene species from the Gulf of California, Mexico, *T. (Tesseropora) uniseimita* (Zullo, 1968: 273), within the proposed classification posed innumerable problems, and consequently I have placed it in a new genus, *Tesseroplax*.

FAMILY TETRACLITIDAE Gruvel

Tétracilitinés Gruvel, 1903: 160; Nilsson-Cantell, 1921: 357, nom. transl.; Ross, 1968: 6, nom. transl.

Definition. — Balanomorpha with shell of 4 plates; rostrum compound; compartments demarcated along sutures on interior surface of wall when fused or corroded externally; parietes with one or more rows of separate or confluent tubes containing living tissue or secondarily filled with calcareous and chitinous material; overlapping plates with radii. Basis membranous or calcareous and not forming complex interdigitations with wall. Inferior margin of mandible pectinate or serrate, never molariform. Labrum not bullate; crest with or without shallow notch, never incised. Cirrus II and III commonly armed with bipinnate and other complex setae distributed along anterior curvature; cirrus III resembling II more than IV; inner or outer ramus commonly antenniform during reproductive cycle. Basidorsal point on intromittent organ, and caudal appendages absent. Occurring in intertidal zone, generally on inanimate objects. Type genus: *Tetraclita* Schumacher, 1817.

Remarks. — Authorship of this family must be accorded Gruvel (1903: 160) rather than Nilsson-Cantell (1921: 357) as earlier noted (Ross, 1968: 6), and the date of authorship accepted as 1903, because "A family group name of which the suffix is incorrect is available with its original date and authorship, but in properly emended form" (Article 11 (e) (ii), ICZN).

INTRA-FAMILIAL RELATIONSHIPS

In the Tetraclitidae shell growth proceeds either diametrically or monometrically (Darwin, 1854: 324). In monometric growth there is a direct correlation between obsolescence of the radii, which are nontubiferous, secondary apical filling of the parietal tubes, and enlargement of the orifice by attrition or corrosion. In diametric growth enlargement of the orifice results directly from growth of the tubiferous radii normal to the parietes without wearing away the peritreme, and the parietal tubes are not secondarily filled.

These modes of shell growth allow separation of the tetraclitids into two groups (Fig. 1). Monometric growth characterizes *Tesseropora*, *Tesseroplax* and *Tetraclita*, diametric growth *Tetraclitella* and *Newmanella*. The latter method is the phylogenetically more primitive based upon the fossil record.

Equally important in segregating the tesseroporan line from the tetraclitellan is the allometry of the carina that occurs commonly in the former group but not the latter. In the tetraclitellans all of the plates develop essentially isometrically. Allometry of the carina and adjacent laterals is a somewhat recent departure from the isometry characteristic of early balanomorphans and is always directly associated with monometric shell growth. Conversely, isometry of the wall plates occurs concomitantly with diametric growth.

Enlargement of the orifice in the tesseroporans, which have monometric shell growth, results from attrition or corrosion of the peritreme, and this is facilitated by their occupancy of a poorly protected high intertidal habitat. In the tetraclitellans enlargement of the orifice is by diametric growth, and this group occurs in relatively well protected habitats low in the intertidal zone. In both groups, the parallel development of a multilayered wall probably confers a selective advantage in that it provides protection against rapacious gastropods and other boring predators.

Tetraclita was probably derived from *Tesseropora*, which retains a single row of parietal tubes. Henry (1957: 36) showed that secondary longitudinal tubules in some individuals of *Tesseropora pacifica* (Pilsbry) is "the first step in the formation of a multilayer wall." She assigned this species to *Tetraclita (sensu stricto)* because of the presence of

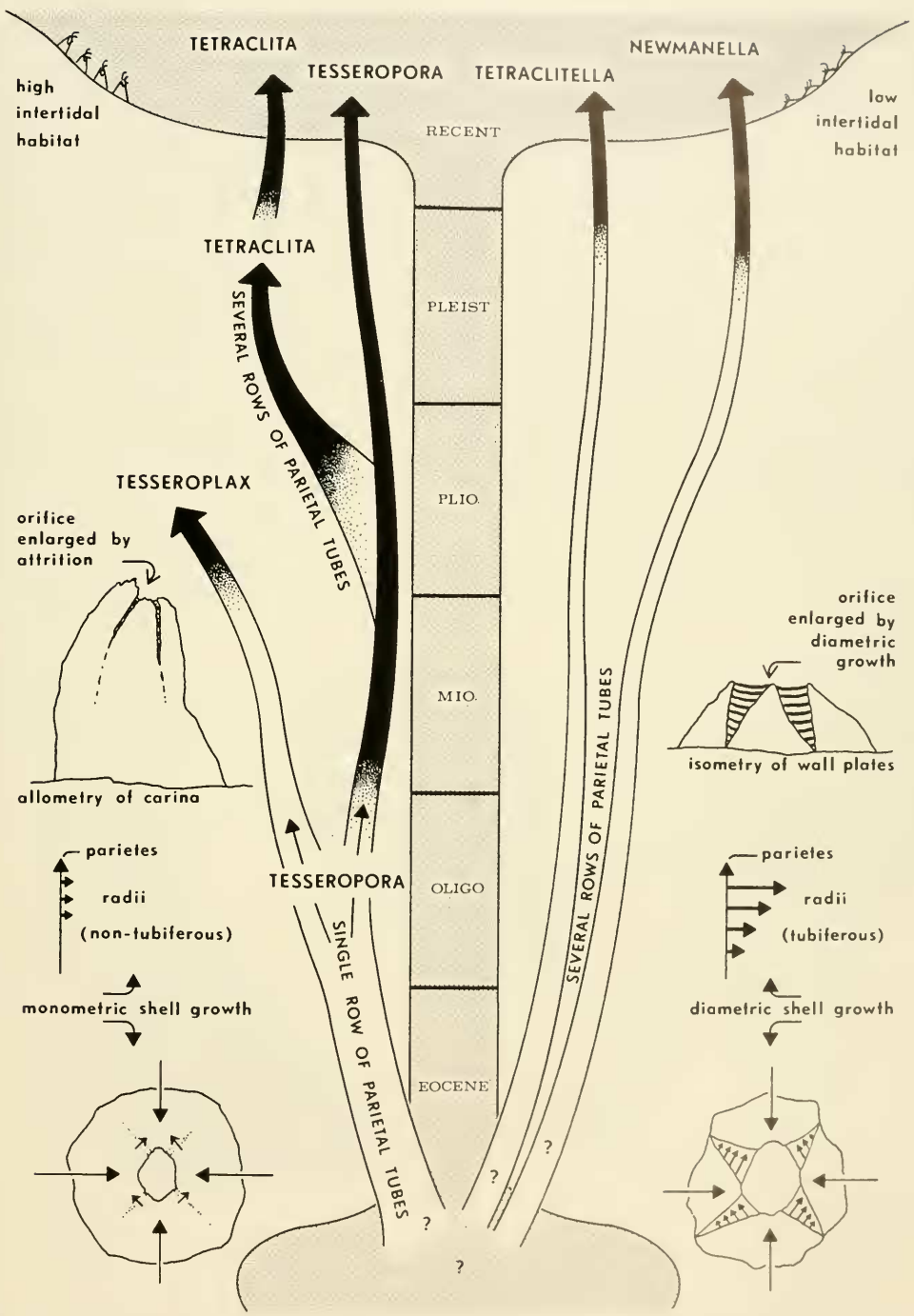


Figure 1. Inferred phylogeny and generic affinities in the Tetracelitidae. Peripheral illustrations portray aspects of shell growth and morphology, and key characters used in distinguishing the two groups in this family.

secondary tubules. However, this assignment is contrary to the original definition of the genus; the secondary tubules are not comparable to those of *Tetraclita*, because there is but one complete row in this species and in certain crowded specimens of *T. rosea* (see Zullo, 1968: 272).

Tesseroplax also has but one row of parietal tubes, and therefore is more closely related to *Tesseropora* than to *Tetraclita*. I regard the absence of depressor muscle crests on the scutum and removal of the tergal spur from the basiscutal angle to be primitive characters in *Tesseroplax* as well as in *Tetraclitella*. The septate parietal tubes in *Tesseroplax* represent a unique specialization for this family, and their function remains unknown, although they may strengthen the wall. *Tesseroplax* probably represents an early off-shoot from the tesseroporan line, as Zullo (1968: 274) suggested, and it is evidently an evolutionary terminus, since none of the presently recognized species can be shown to have evolved from *T. unisemita*. The morphological evidence in support of Zullo's alternate hypothesis that *T. unisemita* may be the result of "convergence on the tetraclitan shell plan from an unrelated ancestor," is weak. The narrow opercular plates in *Tesseroplax*, especially the tergum, may be a direct consequence of monometric growth and allometry in this and other tesseroporans. These attributes strengthen the inference that *Tesseroplax* is in the direct line of descent from *Tesseropora*.

Tetraclitella and *Newmanella* appear to have been derived independently from a tesseroporan precursor, the shell of which had a single row of parietal tubes and developed diametrically. The presence in these genera of two or more rows of parietal tubes, as in *Tetraclita*, I consider a later development which may function as defense against boring predators.

Since each of these tetraclitellans possesses several primitive morphological characters, it is not possible to deduce which genus is more primitive phylogenetically. The scutum in *Tetraclitella*, although elongated, is still basically triangular, and it lacks crests for the insertion of the lateral and rostral depressor muscles. The same is true in *Tesseroplax*. The wall plates in *Tetraclitella* are weakly articulated and do not develop the complex occlusal surface found in *Newmanella*. On the other hand, the tubes in the radii of *Tetraclitella*, to judge from other balanomorphs (e.g., *Megabalanus*, *Emersonius*, *Platylepas*) reflect a highly advanced and complex mode of formation.

KEY TO GENERA OF TETRACLITIDAE

1. Growth of shell monometric; radii solid 2
1. Growth of shell diametric; radii tubiferous 4
2. Parietes with one row of tubes 3
2. Parietes with two or more rows of tubes *Tetraclita*
3. Parietal tubes lacking transverse septa; scutum bearing depressor muscle crests *Tesseropora*
3. Parietal tubes bearing transverse septa; scutum lacking depressor muscle crests *Tesseroplax* gen. nov.
4. Radii with horizontal summits, articular margins lacking teeth; scutum transversely elongated, lacking depressor muscle crests *Tetraclitella*
4. Radii with oblique summits, articular margins bearing prominent teeth; scutum triangular, bearing depressor muscle crests *Newmanella* gen. nov.

Tesseroplax gen. nov.

Definition. — Shell moderately large, smooth; compartments discrete; parietes with one row of rectangular tubes secondarily filled apically, septate basally; radii narrow, non-tubiferous; basis calcareous, with transverse septate tubes; scutum triangular, lacking crests for depressor muscles; tergum narrow, with spur separated from basi-scutal angle.

Type species. — *Tetraclita* (*Tesseropora*) *unisemita* Zullo, 1968.

Etymology. — Derived from the Greek, *tesserēs*, four, and *plax*, plate, in reference to the number of parietal plates.

Remarks. — *Tesseroplax unisemita* is known only from two specimens collected from Pliocene sediments on Angel de la Guarda Island in the Gulf of California, Mexico. Many supposedly unique characters were attributed to this extinct species; but the absence of depressor muscle crests on the scutum is typical of *Tetraclitella*; internal parietal ribs also occur in *Newmanella*; and the apical filling of the parietal tubes is a characteristic of *Tetraclita* as well as *Tesseropora*. However, *Tesseroplax* is the only tesseroporan possessing septate parietal tubes and a calcareous basis also with septate tubes. These structures as well as internal parietal ribs probably reflect a unique method of shell deposition in this lineage. *Tesseroplax* is also the only tesseroporan in which the scutum lacks depressor muscle crests, and the spur of the tergum is infolded as well as being extremely narrow and elongate.

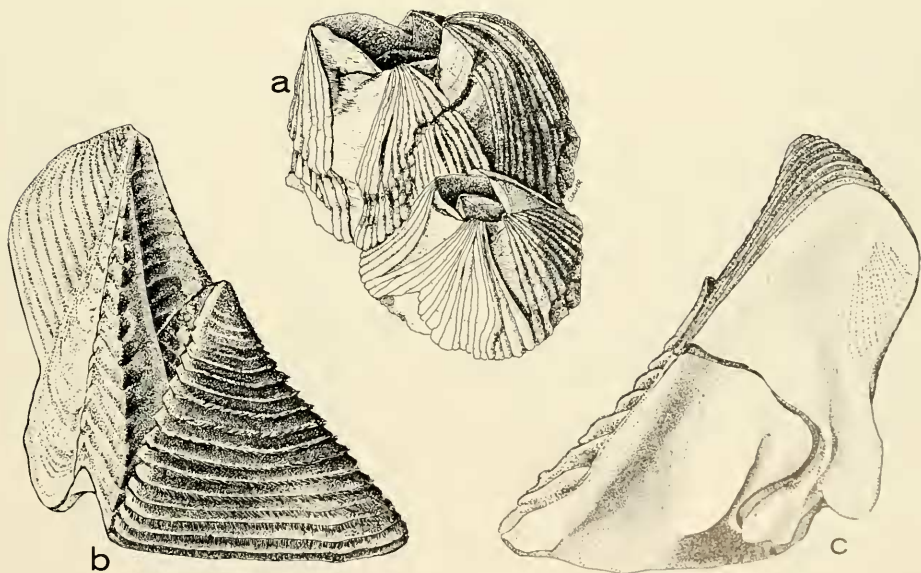


Figure 2. *Newmanella radiata*, from test panel set at 15 m, Vieques Sound, Puerto Rico. a, contiguos specimens viewed from left side, actual height of upper specimen 23.1 mm; b, c, external and internal views, respectively, of articulated opercular plates, actual height of scutum 13.9 mm, tergum 9.5 mm.

Newmanella gen. nov.

Definition. — Shell relatively large, conic, ribbed; compartments discrete; parietes with 2 or more rows of irregularly shaped tubes; radii broad, summits oblique, tubes opening on articular surface; basis calcareous, solid, scutum triangular, bearing crests for depressor muscles; tergum narrow with spur separated from basiscutal angle; mandible with 4 teeth, basal comb, and spine-like lower extremity; maxilla I with more than 12 spines below subapical notch.

Type species. — *Balanus radiata* Bruguière, 1789.

Etymology. — Named in honor of Dr. William A. Newman, Scripps Institution of Oceanography, longtime friend, and student of the Cirripedia.

Remarks. — The presence of more than one row of parietal tubes and well developed tubiferous radii serve to distinguish *Newmanella* from the tesseroporan complex. The radial tubes in *Newmanella* differ from those of *Tetraclitella* by being irregular in outline and of varying size and by their mode of formation, which results from development of prominent irregular ridges on the sutural surface that branch and coalesce. The radial tubes in *Tetraclitella* are uniform in size and outline and develop in a manner comparable to that of the parietal tubes. Initially growth is normal to that of the parietes, but with subsequent growth and sequential development of additional tubes along the outer lamina of the radius, the earlier formed radial tubes curve and may extend downward to the base.

Newmanella radiata (Bruguière)

[*Lepas Indiae orientalis ex violaceo radiata*] Chemnitz, in Martini and Chemnitz, 1785: 319, pl. 99, fig. 842.

Balanus radiata Bruguière, 1789: 168; Bruguière, 1791, pl. 164, figs. 5, 5a.

Lepas purpurea Spengler, 1790: 172.

Lepas violacea Gmelin, 1791: 3213, not *Balanus violaceus* Gruvel, 1903 [= *Balanus abeli* Lamy and Andre, 1932: 218, footnote].

Balanus radiatus: Ranzani, 1818: 75; Lamarck, 1818: 393; Ranzani, 1820: 39; Jay, 1839: 7; Lamy and Andre, 1932: 218.

Conia radiata: Blainville, 1824: 378; Blainville, 1825: 598; Blainville, 1827, pl. 85, figs. 5, 5a; Deshayes, 1831: 357.

T[etraclita] (C[onia]) radiata: Gray, 1825: 104.

Conia lyonsii (ex Leach, MS) Sowerby, 1823, no pagination.

Tetraclita radiata: Darwin, 1854: 343, pl. 11, figs. 5a-5d; Weltner, 1897: 258; Gruvel, 1903: 161; Gruvel, 1905: 291; Schmalz, 1906: 65, pl. 6, fig. 4; Hoek, 1907: xvi; Pilsbry, 1916: 259, pl. 61, figs. 3-3c, 4; Pilsbry, 1927: 38; Nilsson-Cantell, 1939: 5; Pope, 1943: 244; Pope, 1945: 368; Pilsbry, 1953: 27; Southward, 1962: 163; Ross, 1968: 18.

Material. — Turtle Rocks, south of Bimini, Bahamas, B.W.I., approximately 25°40'N., 79°20'W.; intertidal on exposed hull of wrecked ship; E. Kirsteuer coll., August 1967; 5 specimens.

Vieques Sound, Puerto Rico, approximately 18°12'N., 65°25'W.; on fouling test panel set at 15m below surface; U.S. Naval Oceanographic Office, October 1966; 4 specimens.

Vieques Island, Puerto Rico; intertidal; J. A. Rivera and C. B. Rivera coll., November 17, 1951; 10 specimens.

Scotts Head Bay, Dominica, approximately 15°21'40"N., 61°22'40"W.; intertidal on *Tetraclita stalactifera* (Lamarck); E. Kirsteuer and K. Rützler coll., May 17-28, 1966; 1 specimen.

Isla de Margarita, Venezuela, approximately 10°45'N., 64°52'W.; intertidal; P. Glynn coll., May 28, 1968; 7 specimens.

Gulf of Paria, Trinidad, approximately 10°12'N., 61°52'W.; on marine structures in the Shell Trinidad Ltd. oilfield; R. Bacon coll., May 30, 1968; 10 specimens.

Supplementary Description. — Shell white; low-conic; ribs on parietes numerous,

approximate, narrow, prominent, generally branched basally (Fig. 2a). Orifice large, trigonal to pentagonal; peritreme slightly toothed. Radii broad; horizontally striated; summits oblique, at 45° or less; ridges on articular margin irregular, with interspaces forming tubes opening on margin. Alae with summits less oblique than radii; articular margin toothed horizontally. Wall of body cavity with regular longitudinal ribs. Parietes with more than 1 row of irregularly spaced large and small tubes, without definite pattern; longitudinal septa thick, crenated basally. Shell measurements are given in Table 3 of the Appendix.

Basis calcareous; translucent; thin centrally, thickening peripherally.

Scutum triangular; articular ridge high, effectively erect, evenly rounded terminally,

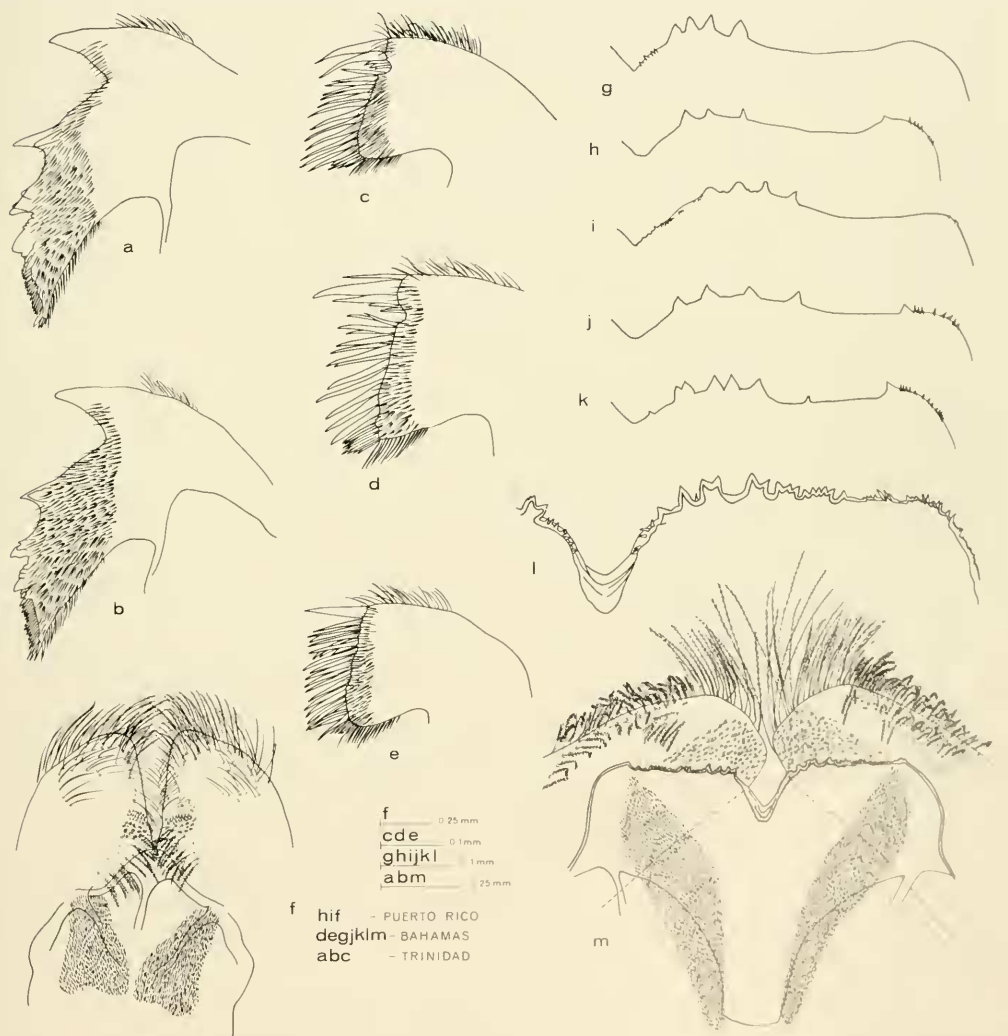


Figure 3. *Newmanella radiata*, trophi. a, b, mandible; c-e, maxilla I; f, maxilla II; g-k, crest of labrum; l, enlarged view of crest of labrum in m; m, labrum and palps.

about $2/3$ length of margin; articular furrow extremely broad and deep; adductor muscle ridge thin, relatively short, apically confluent with articular ridge; adductor muscle depression shallow, poorly defined, crests for lateral and rostral depressor muscles few in number, low, short.

Tergum triangular; longitudinal furrow broad, shallow; spur fasciole open; spur obliquely rounded, separated from basiscutal angle by less than its own width; articular ridge high, projecting and covering apical $1/3$ of scutum when articulated (Fig. 2c); articular furrow broad and deep; crests for depressor muscles numerous, low, regularly spaced.

Crest of labrum with broad V-shaped medial notch either smooth or laterally toothed; teeth on crest either simple, M-shaped or comb-like, numbering commonly 3-4, ranging 2-7 (Figs. 3g-1); superolateral margins of labrum finely serrate or toothed; interspersed among teeth, in notch, and extending laterally along crest of labrum are short, soft bristles. Palps elongate, rectangular; basal margins free of setae; superior margin clothed with short, broad, bipectinate setae; inner lateral face clothed completely with ctenae; distal extremity bearing long, slender, bipinnate setae. Cutting edge of mandible armed with 5 teeth including inferior angle; teeth 2-4 support subsidiary cusps; superior slope of tooth 4 serrate; inferior angle bears 3-4 acicular teeth; comb between tooth 4 and inferior angle contains 17-20 acicular teeth (Figs. 3a-b). Maxilla I with deep, U-shaped notch, rarely without notch; spination along cutting edge in three functional clusters; 2 long, stout spines above notch and 6-9 short, slender spines above or running into notch; 13-20 long, slender spines medially, grading into basal zone of 7-13 short, slender spines. Maxilla II bilobate, taller than broad; setae of apical lobe long, bipinnate, but shorter and bipectinate on lower lobe; region of juncture of two lobes covered with short, narrow spines and ctenae.

Posterior ramus of cirrus I about $2/3$ or less length of anterior ramus; intermediate articles of both rami broader than high; segments of anterior ramus normal, posterior protuberant (Fig. 4a). Rami of cirrus II either essentially equal in length or posterior ramus antenniform (Fig. 4b); terminal segments of anterior ramus armed with few bipinnate setae; proximal and intermediate articles of both rami bullate when cirrus normal. Rami of cirrus III either equal in length or posterior ramus antenniform; when rami are equal, lesser curvature of anterior ramus not covered with spines, and setae are bipectinate; when rami are unequal in length lesser curvature of intermediate and basal segments of both rami covered with short triangular or hook-like spines, and setae bipectinate only on anterior ramus. Cirri IV-VI essentially equal in length with equal rami. Anterior face of posterior ramus of cirrus IV covered with short, triangular spines; proximal segments of both rami along posterior face also spinose. Proximal segments of cirri V-VI covered with short spines along greater curvature only. Chaetotaxis of intermediate articles of cirri IV-VI ctenopod along anterior curvature, with 4 pairs; between or at bases of apical pair are 1-2 short slender setae. Cirral counts are summarized in Table 1 of the Appendix.

Intromittent organ distinctly annulated throughout its length; sparsely hirsute except for 2 distinct clusters surrounding terminal orifice (Fig. 4e).

Remarks. — *Newmanella radiata* is apparently limited to the Caribbean, having been reported from Florida (Pilsbry, 1957: 27), St. Thomas, Virgin Islands (Pilsbry, 1916: 259), and Monos Island, Trinidad (Southward, 1962: 163). New records, which considerably fill gaps in this species distribution include the Bahamas, Puerto Rico, Dominica, and Venezuela.

FUNCTIONAL SIGNIFICANCE OF ANTENNIFORMY

In some individuals both rami of cirrus III are normal, but in others one is normal and one antenniform (setae arranged in whorls at each articulation and the segments articulated

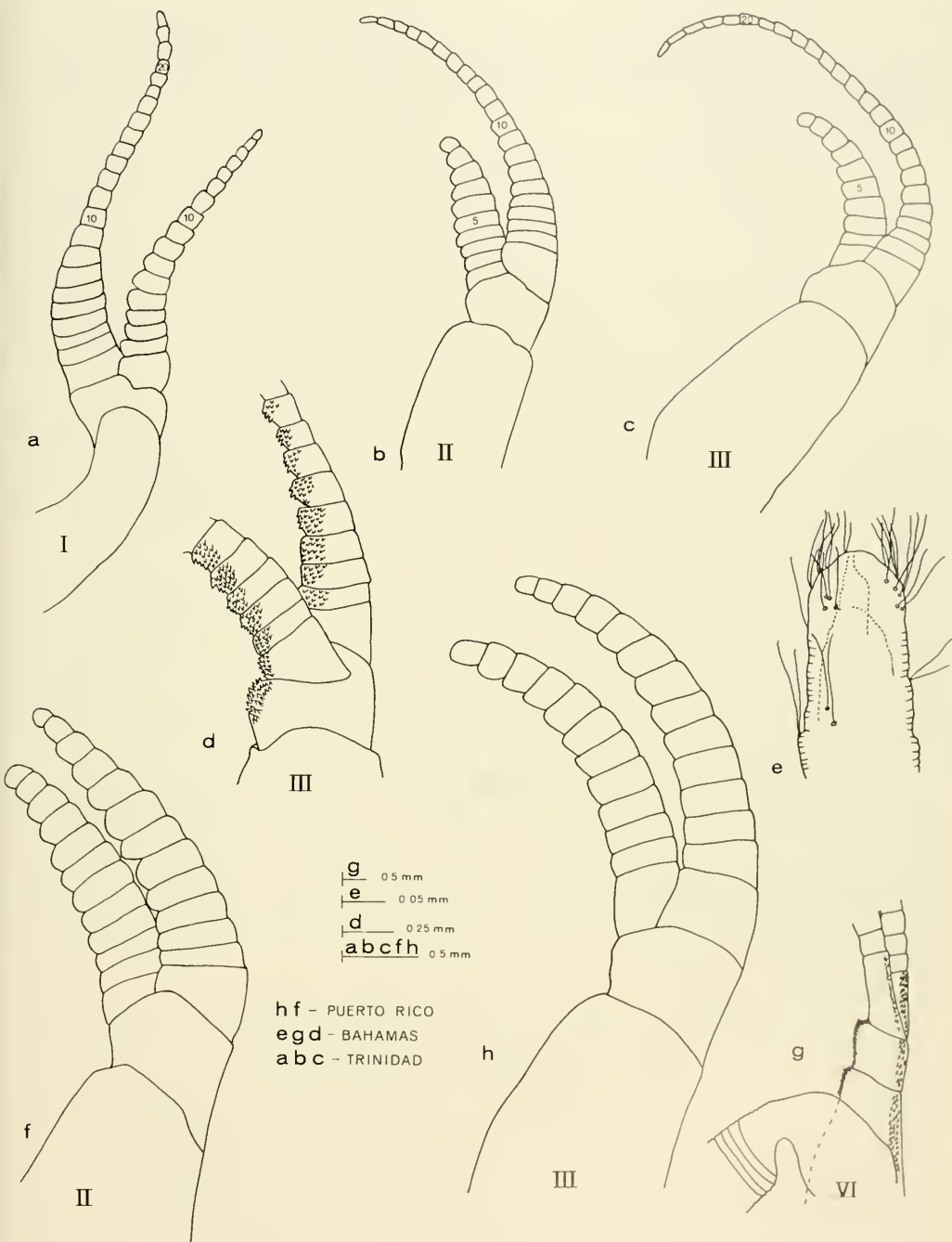


Figure 4. *Newmanella radiata*, cirral appendages. a, left cirrus I; b, left cirrus II with antenniform posterior ramus; c, left cirrus III with antenniform posterior ramus; d, proximal segments of right cirrus III; e, distal end of intromittent organ; f, normal left cirrus II; g, basal segments of left cirrus VI, pedicel, and proximal portion of intromittent organ; h, normal left cirrus III.

so that the ramus can be rotated through 360°). Antenniformy is apparently not widespread in the Chthamalidae, and is unknown in the Balanidae. Of the tetracitid genera recognized herein only *Tetracitella*, to my knowledge, does not exhibit antenniformy, and it is apparently rare in *Tesseropora*.

Darwin (1854: 83) noted variability in the occurrence of an antenniform ramus in chthamalids, and stated that the ramus "acts as an organ of touch." In the deep sea chthamalid *Hexelasma hirsutum* (Hoek), Southward and Southward (1958: 642) found the antenniform ramus to be less sensitive to touch than rami of the other cirri. They noted also that the antenniform rami do not form part of the food gathering cirral net, which would be precluded by the nature of its armament, and speculated that the rami might function as direction indicators, permitting alignment of the net with prevailing food-laden currents. This seems unlikely because individuals with antenniform rami also occur in intertidal habitats, where there is no obvious adaptive value for such an organ.

Pope (1965: 59) detected no correlation between the presence or absence of an antenniform ramus and age, seasonal or environmental variables. However, seventy per cent of the eastern Australian population of *Chthamalus antennatus* Darwin that she studied, had antenniform rami, and 80 per cent of the total population were brooding. Specimens collected three weeks later from the same area had normal rami, but only 20-35 per cent still contained developing nauplii. At no time did all individuals in the population have antenniform rami.

In *Newmanella*, the May specimens from Venezuela had antenniform rami and were brooding nauplii, but the opposite was true of specimens collected from Dominica and Trinidad, except for one individual from Trinidad that had antenniform rami. Specimens taken in August from the Bahamas and in October and November from two localities off Puerto Rico also lacked antenniform rami and eggs or nauplii in the mantle cavity (Fig. 5). Development of the antenniform ramus in *N. radiata* probably begins in February or March, and the appendage is shed in April or May only to be replaced by a normal ramus.

Specimens of *Tetrachthamalus obliteratus* from Mauritius were found to have normal rami, and one individual was brooding; those from Elat, and all but one from Seychelles, had antenniform rami, and both populations were brooding eggs or nauplii (Newman, 1967: 430; pers. comm.). Newman also observed that individuals with antenniform rami either lack or have a diminutive intromittent organ, whereas individuals with normal rami have a normally developed intromittent organ. In *Tesseropora pacifica* from Guam I have observed the simultaneous presence of an antenniform ramus, reduced intromittent organ, and eggs in the mantle cavity.

According to Crisp and Patel (1958: 1078) copulation and fertilization commonly follow within a few days of ecdysis. However, ecdysis early in the reproductive cycle normally results in loss of the recently oviposited eggs, because they lie in the mantle cavity, the lining of which is molted with exuviae of the appendages, intromittent organ, prosoma, esophagus, and rectum (Darwin, 1854: 157). Consequently, newly fertilized individuals normally cease molting during the brooding period, which lasts for several weeks. But, if the molting process is resumed after fertilization but prior to naupliar release, the mantle lining is retained and complete exuviation either accompanies or follows liberation of the nauplii (Patel and Crisp, 1961: 103). In *Balanus balanoides* Linnaeus the intromittent organ is lost during exuviation after the time of fertilization, whether the individuals have been fertilized or not (Crisp and Patel, 1960: 33). A new one gradually develops during the summer, reaching a normal length prior to the onset of the breeding season, which in *B. balanoides* occurs annually in November or December; development of the intromittent organ in *Tetrachthamalus* and *Tesseropora pacifica* probably follows a similar pattern as does the

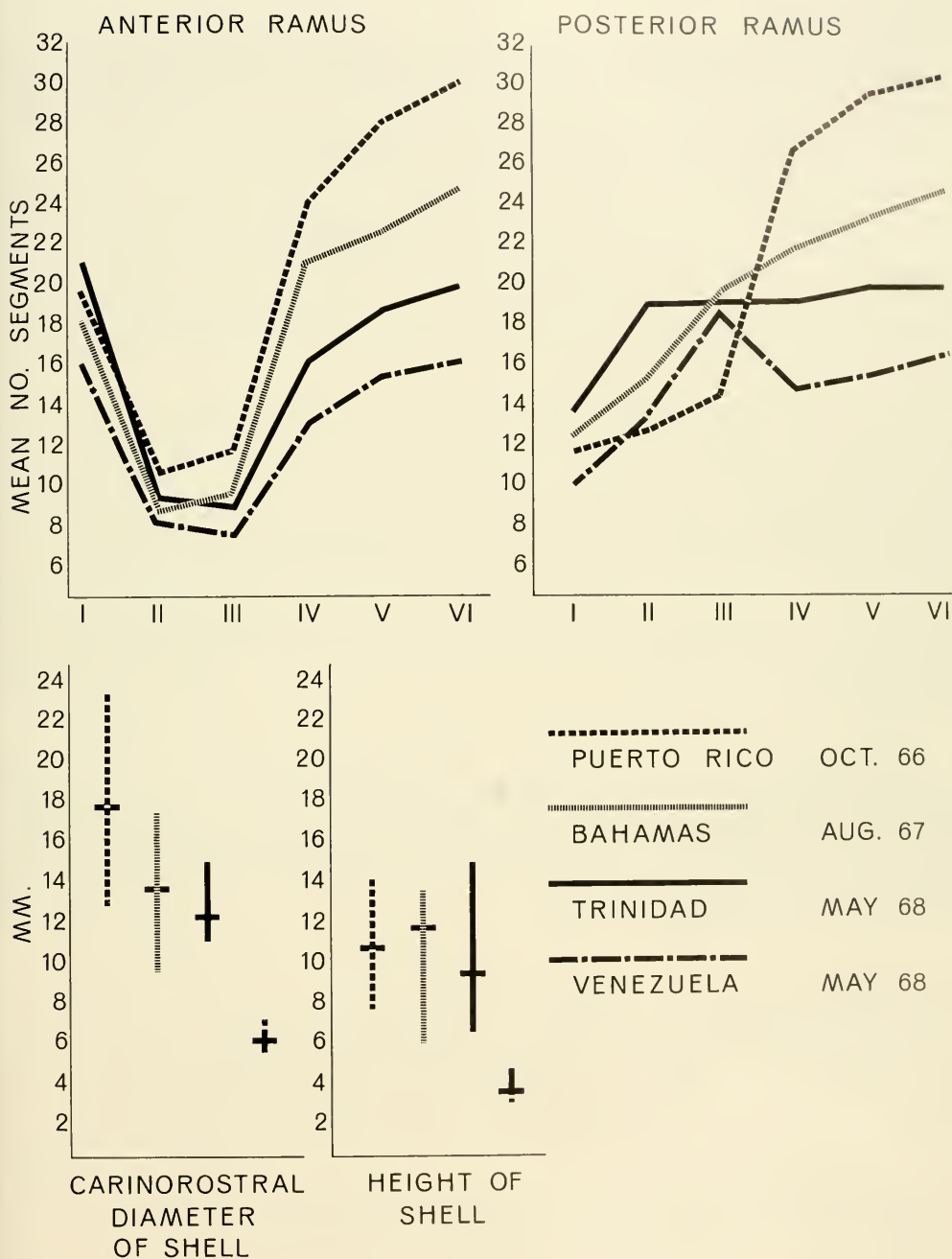


Figure 5. Graph of mean values from Table 1 for cirral counts of anterior ramus (top left) and posterior ramus (top right), and from Table 3 for carinorostral diameter of shell (bottom left) and height of shell (bottom right) of *Newmanella radiata*. Vertical line = range; horizontal bar = mean.

antenniform ramus.

Thus, there is a strong correlation between the reproductive period and the presence of antenniform rami. In all cases, antenniform rami are noted first either immediately before, during, or immediately after the reproductive period, which may occur more than once a year in the chthamalids and tetracitids. The presence of an antenniform ramus has not been reported in individuals long after termination of the reproductive cycle.

In cross-fertilizing intertidal balanomorphs copulation takes place while the animals are submerged. Some means of indicating copulatory availability would be advantageous during this phase of the reproductive cycle, because these animals are monoecious and every individual in the population is potentially capable of being fertilized by another nearby individual. Since the periods of submergence are usually brief, some adaptation would be effective in insuring rapid selection of a responsive individual. The antenniform ramus may elicit or detect tactile or chemical stimuli from an individual acting the role of the opposite sex.

The correlation between brooding, antenniformy, and penis development is complicated. However, it appears that individuals brooding eggs or nauplii, having antenniform rami, and lacking or having diminutive penes assume the morphology and act the role of a female; those individuals without eggs or nauplii in mantle cavity, and with normal rami and penes constitute the post-reproductive segment of the population, having reverted to the normal hermaphroditic state. Resumption of the hermaphroditic state is necessary because these animals will cross-fertilize during the next breeding season. Loss or diminution of the intromittent organ after fertilization is not comparable to the loss of the antenniform ramus after release of the nauplii, because the ramus is replaced by a functional, feeding appendage, whereas the intromittent organ remains non-functional until the onset of the following breeding season.

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APPENDIX

MEASUREMENTS FOR *NEWMANELLA RADIATA*

Table 1. Summary of data on cirral counts: range (R) and mean (X) values for the number of segments in anterior (a) and posterior (p) rami.

	I		II		III		IV		V		VI		
	a	p	a	p	a	p	a	p	a	p	a	p	
Bahamas	N	10	10		10	10	10	10	10	10	8	9	
	R	18-23	10-15	7-9	12-19	8-12	11-24	20-24	20-24	19-25	20-25	24-26	22-26
	X	18.20	12.20	8.40	15.30	9.10	19.3	21.30	21.70	22.50	23.20	24.88	24.67
Vieques Sound Puerto Rico	N	8	8	8	7	8	7	6	6	6	6	4	6
	R	19-21	11-14	7-13	11-14	8-14	12-17	20-28	23-30	24-33	25-34	26-35	26-34
	X	19.75	12.00	10.37	12.71	11.62	14.57	24.00	27.00	28.00	29.66	29.75	30.16
Venezuela	N	5	7	8	8	8	7	8	7	7	7	7	8
	R	14-18	9-11	6-13	8-21	6-8	14-21	12-15	13-16	13-18	14-17	14-18	14-18
	X	16.00	10.00	8.00	13.25	7.25	18.42	13.38	14.43	15.14	15.14	16.14	16.25
Trinidad	N	8	8	8	8	8	5	8	9	8	7	7	9
	R	16-25	8-17	7-10	16-22	7-11	12-25	13-19	16-23	16-20	17-24	17-24	16-25
	X	21.00	13.62	8.75	18.50	9.00	19.00	16.38	19.00	18.50	19.85	19.85	19.88

Table 2. *Cirral counts for individual specimens.*

Dominica		I	II	III	IV	V	VI
right	Anterior	19	9	11	14	17	15
	Posterior	13	17	21	13	15	14
left	Anterior	18	9	9	12	14	14
	Posterior	12	16	11	12	13	14
Vieques Island, Puerto Rico							
right	Anterior	22	12	15	27	37	37
	Posterior	14	20	23	34	37	36
left	Anterior	22	13	15	26	33	27
	Posterior	15	19	18	31	38	39

Table 3. *Summary of data on shell and opercular valve parameters (in mm): range (R) and mean (X) values.*

		SHELL			OPERCULAR PLATES			
		Car-Ros			Scutum		Tergum	
		Diam.	Lat. Diam.	Height	Height	Width	Height	Width
Bahamas (n = 5)	R	9.3-17.2	9.5-16.5	5.9-13.3	2.5-4.8	2.5-4.9	3.4-6.1	2.3-4.5
	X	13.4	12.7	11.4	4.2	4.3	5.3	3.8
Vieques Sound, P.R. (n = 4)	R	12.9-23.1	13.3-24.6	7.5-13.9	4.6-6.6	4.1-7.0	6.1-9.5	4.3-7.6
	X	17.6	17.8	10.4	5.5	5.2	7.5	5.7
Venezuela (n = 6)	R	5.4-7.2	5.1-7.1	2.6-4.5				
	X	5.9	6.0	3.0				
Trinidad (n = 5)	R	11.1-14.9	9.4-14.5	6.1-14.7	3.0-6.8	2.7-6.1	3.5-7.4	2.6-5.0
	X	12.1	9.8	9.3	4.3	4.0	4.8	3.3
Dominica (n = 1)		10.0	8.1	7.8	3.1	2.9	3.5	2.6
Vieques Island, P.R. (n = 1)		31.3	29.3	28.1	10.1	10.5	13.1	13.9